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Disappearance of Icelandic Walruses Coincided with Norse Settlement

Xénia Keighley ^{1,2,3}, Snæbjörn Pálsson,⁴ Bjarni F. Einarsson,⁵ Aevor Petersen,⁶ Meritxell Fernández-Coll,^{4,7} Peter Jordan,³ Morten Tange Olsen,^{*,1,2} and Hilmar J. Malmquist⁷

¹Section for Evolutionary Genomics, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark

²Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

³Arctic Centre and Groningen Institute of Archaeology, University of Groningen, Groningen, The Netherlands

⁴Faculty of Life and Environmental Sciences, University of Iceland, Reykjavik, Iceland

⁵The Archaeological Office, Reykjavik, Iceland

⁶Reykjavik, Iceland

⁷Icelandic Museum of Natural History, Reykjavik, Iceland

*Corresponding author: E-mail: morten.olsen@bio.ku.dk.

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Abstract

There is a growing body of evidence demonstrating the impacts of human arrival in new “pristine” environments, including terrestrial habitat alterations and species extinctions. However, the effects of marine resource utilization prior to industrialized whaling, sealing, and fishing have largely remained understudied. The expansion of the Norse across the North Atlantic offers a rare opportunity to study the effects of human arrival and early exploitation of marine resources. Today, there is no local population of walruses on Iceland, however, skeletal remains, place names, and written sources suggest that walruses existed, and were hunted by the Norse during the Settlement and Commonwealth periods (870–1262 AD). This study investigates the timing, geographic distribution, and genetic identity of walruses in Iceland by combining historical information, place names, radiocarbon dating, and genomic analyses. The results support a genetically distinct, local population of walruses that went extinct shortly after Norse settlement. The high value of walrus products such as ivory on international markets likely led to intense hunting pressure, which—potentially exacerbated by a warming climate and volcanism—resulted in the extinction of walrus on Iceland. We show that commercial hunting, economic incentives, and trade networks as early as the Viking Age were of sufficient scale and intensity to result in significant, irreversible ecological impacts on the marine environment. This is to one of the earliest examples of local extinction of a marine species following human arrival, during the very beginning of commercial marine exploitation.

Key words: palaeogenetics, extinction, human impacts, exploitation, *Odobenus rosmarus*, Viking Age.

Introduction

A growing body of research has debated the role of humans in triggering dramatic ecological changes following their arrival in otherwise “pristine” ecosystems (Fitzpatrick and Keegan 2007; Lorenzen et al. 2011; Allentoft et al. 2014; McCauley et al. 2015; Braje et al. 2017). Evidence for both environmental degradation (including deforestation and erosion) and population collapse of terrestrial species, has largely focused on the successive phases of human arrival to Pacific islands (Jackson et al. 2001; Nagaoka 2002; Hunt and Lip 2006; Erlandson and Rick 2010), or continental Europe, North America and Australia with respect to Pleistocene megafauna extinctions (Nogués-Bravo et al. 2008; Sandom et al. 2014; Faurby and Svenning 2015). However, research into the ecological impacts to marine environments prior to early commercial exploitation in the Late Middle Ages has been extremely limited (Malakoff 1997; Anderson 2001; Erlandson and Rick 2010; Dunne et al. 2016). Iceland offers

a rare opportunity to explore the effects of human arrival on marine ecosystems at the very beginning of intensified commercial European exploitation.

The Norse of the Viking Age (~700–1050 AD) were the first people to settle permanently in Iceland around 870 AD (Eldjárn 1956; Einarsson 1995, 2019; Batt et al. 2015; Zori 2016). Norse exploration and settlement of the sub-Arctic and Arctic North Atlantic was likely driven by desires to find resources for trade and reciprocity, arable land, and an escape from ruling power in Scandinavia (Einarsson 2011, 2015; Hambrecht 2015; Zori 2016). Icelandic medieval literature recounts the progressive settlement of the Norse in the Faroe Islands, Iceland, Greenland, and Vínland (North America) (Barraclough 2012; Murray-Bergquist 2017). These records, written much later in the 12–14th centuries (Smith 1995; Hartman et al. 2016), present little information about the exploitation of marine resources, such as fish, seabirds, and marine mammals. However, modern interpretations

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based on archaeological findings and historical sources suggest that reliance on marine resources for both subsistence (e.g., fish consumption) and trade (e.g., walrus ivory) was previously underestimated (Guðmundsson 1997; Pierce 2009; Birgisson 2013; Einarsson 2015; Frei et al. 2015). Recent studies have highlighted the importance of valuable goods from both marine and terrestrial sources traded from Iceland and Greenland to medieval Europe, such as furs or the hide, meat, fat, and ivory from walrus (*Odobenus rosmarus* Linnaeus 1758) (Guðmundsson 1997; Birgisson 2013; e.g., Keller 2010).

Although it is still debated whether trade, farming or politics drove Iceland's initial settlement, its long-term success rose from farming and the development of a trade economy. Trade was based upon natural resources, with an emphasis on stockfish and wool during later phases after settlement (Perdikaris and McGovern 2007; Hartman et al. 2017). Already during the settlement period (870–930 AD), dramatic environmental changes, including deforestation and soil erosion, occurred in some regions (Vésteinsson et al. 2002). These changes have been attributed to exploitation, grazing, and natural causes including volcanic activity (Smith 1995; Dugmore et al. 2005). Compared with the impact of Norse settler activities on the terrestrial environment, anthropogenic impacts on marine ecosystems, and the importance of maritime resources in the earliest postsettlement phase, is less clear (Ólafsdóttir et al. 2014). Some historians and archaeologists have suggested the loss of walruses as one dramatic change due to human hunting in the Settlement period (Dugmore et al. 2007; Frei et al. 2015). This has been challenged by claims that walruses had already disappeared well before the arrival of the Norse (Einarsson 2011), most likely due to volcanic or environmental disturbance. However, conclusive evidence relating to the abundance, distribution, and genetic identity of Icelandic walruses, as well as the extent and potential impact of human hunting, has been lacking.

Direct evidence of walrus populations in Iceland has been limited to finds of prehistoric tusks, skulls, and bones found at sites of coastal erosion, dredging, construction work, or archaeological excavations (Petersen 1993; this study) (Vésteinsson et al. 2002; McGovern 2013) and several old Icelandic place names referring to walruses (Thoroddson 1911; Kristjánsson 1986; Einarsson 2011). However, it is unclear whether these remains and place names refer to vagrant walruses, surface finds of ivory from a local walrus population lost well before Norse arrival, or a unique local population hunted to extinction after settlement (Roesdahl 2003; Hartman et al. 2017). Biomolecular analyses offer the potential to answer these questions by providing radiocarbon dating, geographic origin, and genetic characterization of Icelandic walruses. However, studies have been limited to a single pilot isotopic study, revealing a unique stable lead isotopic signature in Icelandic walrus (Frei et al. 2015), and an ancient DNA study documenting an overall transition in ivory sources from the eastern to western North Atlantic (Star et al. 2018).

In this study, we compiled lists of old place names, skeletal finds, and written records (from 870 to 1262 AD) referring to

walruses in order to assess the spatiotemporal occurrence of walrus in Iceland. Of the known walrus skeletal finds, a total of 34 were available for destructive analysis and subject to radiocarbon dating. We generated mitochondrial DNA sequences from these dated samples and additional historic and ancient walruses from across the North Atlantic. We then combined and analyzed the newly generated genetic data with previously published genetic sequences totaling 67 mitochondrial genomes, as well as >400 control region (CR) sequences, to reveal the phylogenetic placement of Icelandic walruses and the potential impact of Norse hunting on the population.

Results and Discussion

A Unique Genetic Lineage of Icelandic Walruses Existed Prior to Norse Settlement

Skeletal remains, place names, radiocarbon dates, and ancient mitochondrial DNA analyses support the existence and continuous occupation of a unique resident Icelandic walrus population for thousands of years prior to the arrival of the Norse. Radiocarbon dated samples revealed an almost continuous chronology of walrus concentrated in western Iceland for about 7,500 years (fig. 1), suggesting a stable, long-term presence of walrus in Iceland up until 1213–1330 AD (supplementary material 1, Supplementary Material online). This evidence supports the Norse as active hunters of a local population of Icelandic walruses and not opportunistic collectors of prehistoric ivory fragments. The existence of walrus on Iceland during early Norse settlement was further supported by eight place names referring with certainty to walruses originating from the Settlement (870–930 AD) and Commonwealth (930–1262 AD) periods (supplementary material 2, Supplementary Material online). In addition, walrus skeletal remains have been identified from a total of 224 known and five unknown locations, often clustered at the same or nearby locations in western Iceland (e.g., Reykjavík city [17 finds], Akranes town [8 finds], and Flatey island, Bay of Breiðafjörður [8 finds]) (fig. 2). Approximately 68% of all 229 find featured single tusks, a further 24% included skulls with tusks and the remaining ~8% comprised skulls without tusks or other bones (e.g., mandibles, baculum, ribs).

The concentration of place names and skeletal remains in western Iceland corresponds well with potential walrus habitat and food requirements. Indeed, Iceland's northern and western coasts have extensive shallow-water coastlines with a large number of fjords, islets, and banks suitable for hauling-out. These areas also support well-established benthic communities (Óskarsson 1982; Ingólfsson 1996; Simonarson 2004; Simonarson and Leifsdóttir 2009), rich in three of the most important bivalve species for contemporary Atlantic walrus (*Hiatella arctica* Linnaeus 1758, *Mya truncata* Linnaeus 1758, and *Serripes groenlandicus* Mohr 1786; Vibe 1950; Fisher and Stewart 1997; Born et al. 2003). All three mollusc species are known to have existed in Iceland for several million years (Simonarson and Leifsdóttir 2009).

Phylogenetic analysis of mitochondrial genomes showed strong support for all Icelandic walruses within the Atlantic

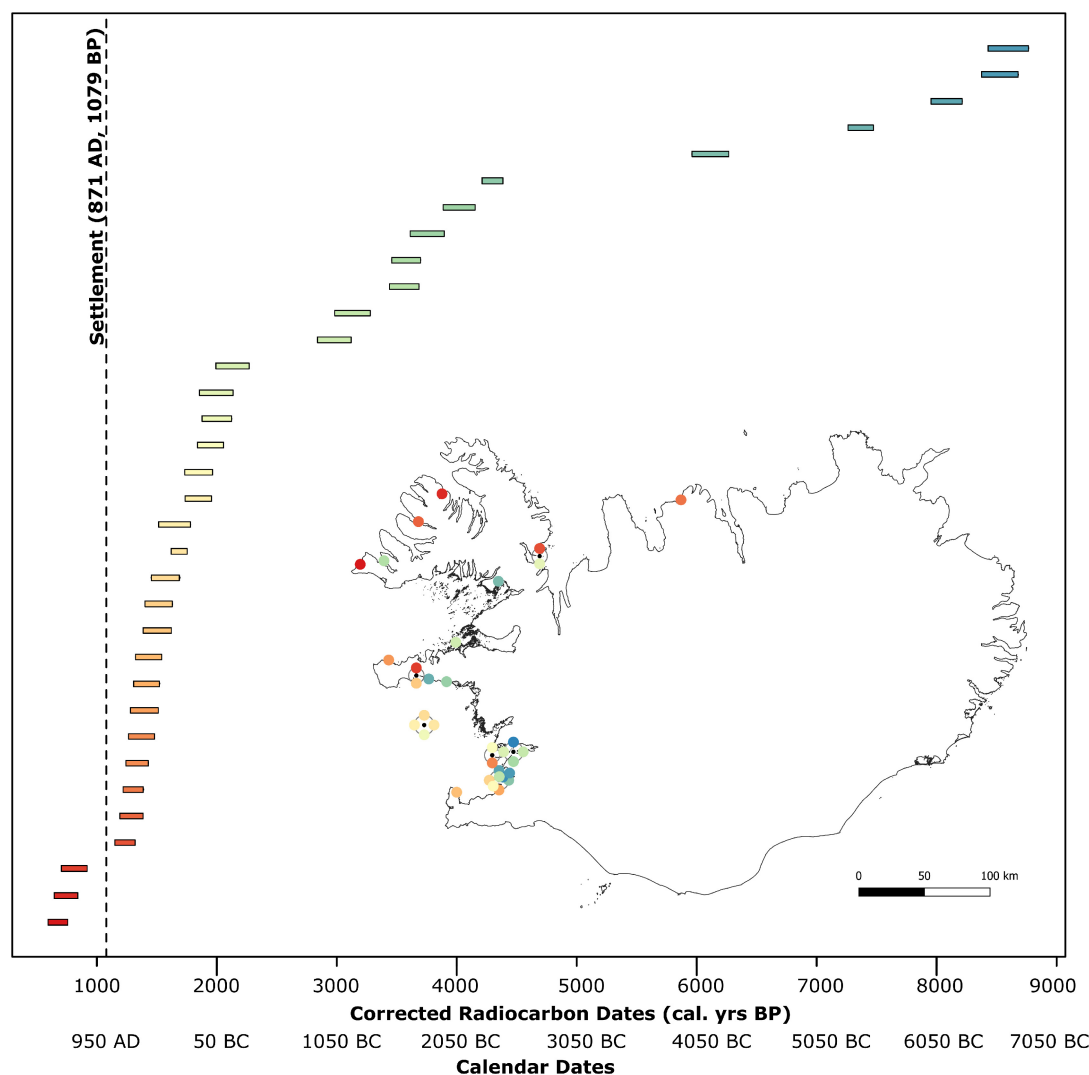
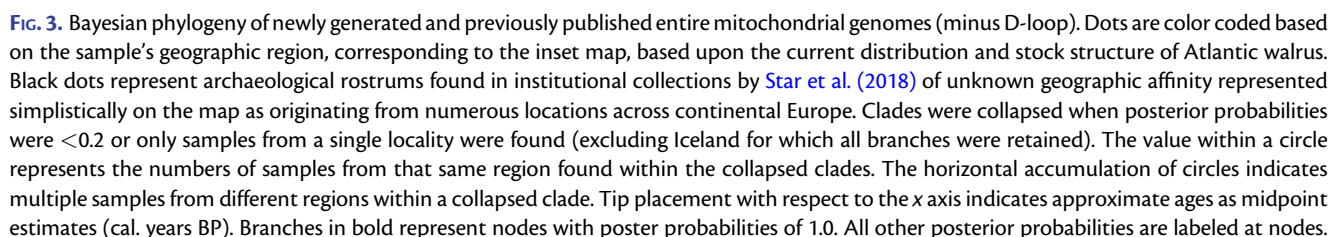
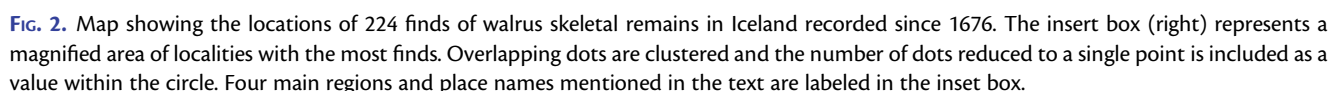


Fig. 1. Location (inset map) and age (graph) of Icelandic samples with successful radiocarbon dates included in this study ($n = 34$). Graph: Horizontal bars show represent 95.4% confidence intervals of marine reservoir corrected radiocarbon dates for all successfully dated Icelandic samples (y axis). Dates on the x axis are presented as both calibrated years BP (1950 AD) (top row) and calendar dates (bottom row). Midpoint range across all samples is 1290–8599 years BP. The black vertical dashed line represents Icelandic settlement around 870 AD (1080 BP). Bars are color coded based on age and correspond with sample dots on the map indicating collection localities. Map: Localities of sample provenance are indicated by colored points. Any overlapping points are offset by cluster grouping (indicated by a central black dot and overlapping circles displayed in a surrounding circle).

subspecies *O. rosmarus rosmarus* (Linnaeus 1758) (fig. 3). Two distinct clades were found within Atlantic walruses, as per Star et al. (2018); the first containing only samples from the Western North Atlantic (hereafter *western*), the second including samples from across the North Atlantic (hereafter *mixed*). The five most recent Icelandic mitochondrial genomes formed a monophyletic group within the *mixed* clade, whereas the oldest Icelandic sample (5502–5332 BCE) was found basal to all samples within the *mixed* clade. The distinctiveness of this oldest sample suggests that phylogenetic affinity of ancient Icelandic walruses was different to historical samples. However, with only a single successful ancient Icelandic sample, it cannot yet be determined whether there have been cycles of lineage turnover, recolonization due to glaciation (see Geirsdóttir et al. 2007) or volcanic events

(see Thordarson and Larsen 2007), or a very different pan-Atlantic population structure for walruses earlier in the Holocene.

The genetic uniqueness of Icelandic walruses was further confirmed by comparing 26 newly generated Icelandic mitochondrial CR sequences with 58 previously published walrus CR haplotypes, in total representing >400 contemporary and historic walruses sampled throughout the North Atlantic (fig. 4). Icelandic walruses had eight unique haplotypes which clustered together, and were not shared with any extant walruses. Distance matrices based on Φ_{ST} values indicate Icelandic CR haplotypes were the most differentiated relative to all other populations, with distances ranging from 0.47 (Franz Josef) to 0.91 (Canadian Maritimes) ($P < 0.001$) (supplementary materials 3 and 4, Supplementary Material



Iceland. CR data were also used to infer past demographic history with an Extended Bayesian Skyline Plot ([supplementary material 6, Supplementary Material](#) online). The results from this plot were inclusive, suggesting either a stable population or a more complex population trajectory that is not discernible given high levels of statistical uncertainty.

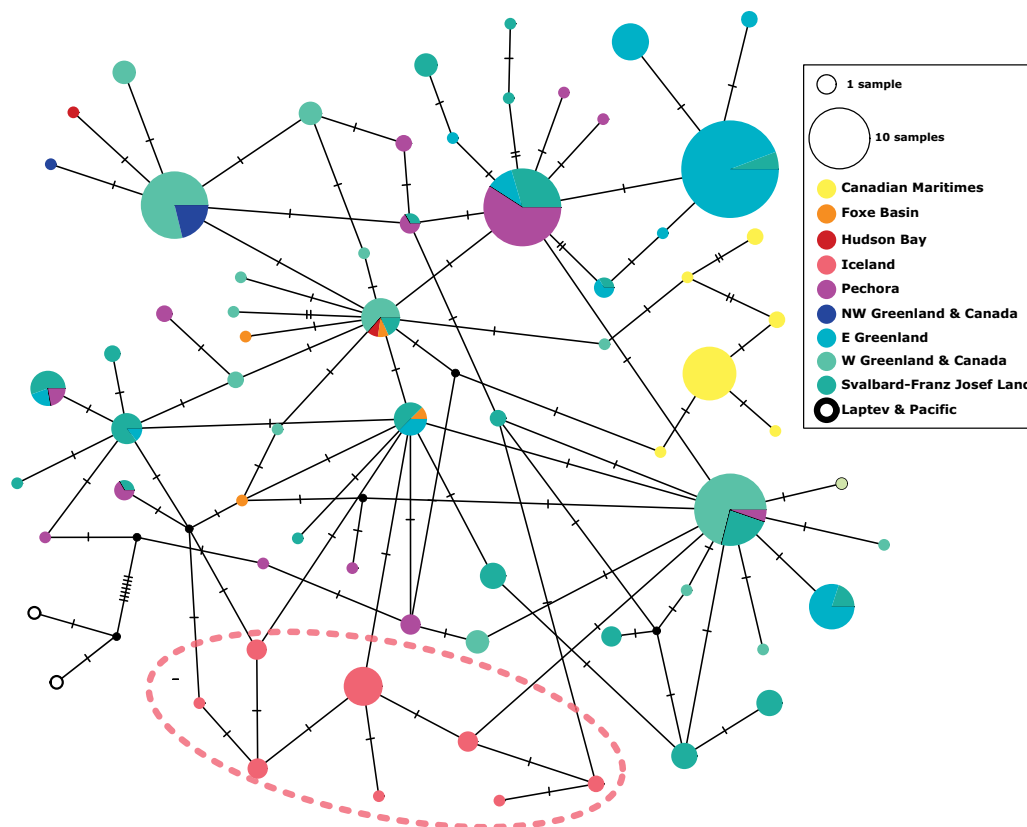


FIG. 4. Haplotype network from SANGER-sequenced newly generated and previously published mitochondrial CR sequences. Circles are color-coded according to the geographic origin of samples (coloration corresponds with [fig. 3](#)). Icelandic samples fall into a cluster of eight unique haplotypes (circle by a dashed line). Only samples with a maximum of one missing or ambiguous base were included to avoid erroneous haplotype assignment. Haplotype assignment was repeated for samples with missing data for a shortened region of the mitochondrial CR, resulting in eight of the nine previously unassigned samples sharing one of the second most common Icelandic haplotypes.

Insights into the Norse Hunt and Trade of Walrus from Written Records and Place Names

Although written well after settlement, in the 12th–13th centuries, Icelandic medieval literature provides some information on the hunt and use of walrus in early Norse Icelandic society ([Rafnsson 1974](#); [Friðriksson and Vésteinsson 2003](#)). The oldest, most detailed, and certain written account of an Icelandic walrus hunt is found in the Saga of Hrafn Sveinbjarnarson (written in the late 12th century and occurring in *Dýrafjörður*; Westfjords). In this account, a wounded walrus escaped back to sea before being successfully hunted with the aid of chieftain Hrafn ([Biskupasögur 1858](#)). Hrafn subsequently set sail to bring the skull and both tusks to Canterbury cathedral in honor of St. Thomas á Becket ([Biskupasögur 1858](#)). This account highlights the value of walrus ivory during the Viking Age. Further mention of field trips to the northern Westfjords to procure “whales and other resources” is mentioned in *Grettissaga* (9th–11th century AD) and *Fóstbræðrasaga* (early 11th century AD). Discussion of other place names potentially referring to walrus is included in [supplementary material 2, Supplementary Material online](#).

Hunts sought to obtain walrus meat, hide, and blubber for domestic use, but also ivory as a nonperishable, easily transportable, highly valuable trade good for international markets ([Roesdahl 2003](#); [Seaver 2009](#); [Keller 2010](#); [Star et al.](#)

[2018](#)). Across Europe, the Middle East, and Asia, walrus ivory was crafted into a wide range of objects including ecclesiastical crosiers, game pieces ([Roesdahl 2003, 2015](#); [Dectot 2018](#)) and most particularly, sword hilts and knife handles ([Laufer and Pelliot 1913](#); [Seaver 2009](#); [Gillman 2017](#)). Icelandic ivory was included in this international trade, with our results revealing that one previously published mitochondrial genome ([Star et al. 2018](#)) from an 11th century tusk offcut excavated in Sweden, clustered with this study’s Icelandic samples. However, the contribution of Icelandic ivory to medieval European markets was most probably small ([Pierce 2009](#)), particularly in comparison to western Greenland as the major focus of walrus hunting efforts from mid-12th–15th centuries ([Star et al. 2018](#)).

The Fate of the Icelandic Walrus?

The question therefore emerges as to why and how Icelandic walrus disappeared? Was Norse hunting, environmental factors, or a combination of both, responsible for the loss of Icelandic walrus? Did the local population of walrus become extinct or did they move to surrounding areas eventually interbreeding with other North Atlantic walrus populations?

The hypothesis of dispersal would be congruent with historic observations of walrus responding to human

disturbance (Wiig et al. 2007; Lydersen et al. 2008). However, the present study found no genetic evidence for major population movement from Iceland to surrounding populations (Eastern Greenland, Franz Josef Land, or Svalbard). There was no shared CR haplotype or mitochondrial genome affinity between Icelandic walruses and any modern or ancient Atlantic walruses. Extinction is therefore the most probable explanation.

The extinction of Icelandic walruses was likely caused by human hunting given the timing, known value of walrus during the Viking Age, and how easy naïve Icelandic animals were to capture, as mentioned in several Sagas (Vésteinsson et al. 2002; Hartman et al. 2016; Murray-Bergquist 2017). Exacerbating the effect of human hunting, environmental factors including volcanism and a warming climate may also have contributed to the disappearance of Icelandic walrus. As a volcanically active island, Iceland experienced 57 eruptions during the Settlement and Commonwealth periods (870–1262 AD) (Thordarson and Larsen 2007). Several of these were of considerable size and impact, including the Hallmundarhraun lava flow (~950 AD, western Iceland), and the Great Eldgjá flood lava eruption (934–938 AD southern Iceland) (Thordarson and Larsen 2007). This last eruption in particular, led to widespread tephra fall and substantial air pollution (Larsen 2000; Thordarson et al. 2001), which may have directly and indirectly impacted animals, including walrus. Indeed, more recent eruptions of a similar size have resulted in illness and mortality for various animals (Thorarinsson 1979; Thordarson and Self 1998; Schmidt et al. 2011). Walrus prey and/or habitat may also have been negatively impacted by smaller volcanic events when they occurred close to key haul-out sites, such as Reykjanes peninsula and surrounds (Einarsson and Jóhannesson 1991; Sinton et al. 2005). For example, more recent eruptions off the Reykjanes peninsula at the start of the 19th century are considered a contributing factor in the demise of Great Auk (*Pinguinus impennis*), which was hunted to extinction later that century (Garðarsson 1984; Petersen 1995; Fuller 1999).

In addition to volcanism, climatic factors may also have made walrus populations more vulnerable and less resilient to anthropogenic stressors. Climatological and oceanographic studies indicate that the North Atlantic, including Iceland, experienced a relatively warm climate with minimal sea-ice during the time of Norse expansion (~700–1100 AD) (Ogilvie et al. 2000). A warmer climate may have limited walruses to terrestrial haul-out sites, reduced their ability to mate or feed (Kovacs et al. 2015) and increased their exposure to human hunting (Born et al. 1995; Born et al. 2017). The potential role of volcanic or climatic factors in triggering population declines in Icelandic walrus prior to Norse arrival could not be resolved with an Extended Bayesian Skyline Plot, with equally valid interpretations possible of both a stable population or change in population demography hidden by large levels of statistical uncertainty (supplementary material 6, Supplementary Material online). Therefore, although the contribution of climatic and volcanic activity cannot be quantified with current data in the eventual demise of Icelandic

walrus, the timing of walrus extinction suggests an important anthropogenic effect.

There are a growing number of examples documenting species and population collapses following human arrival in new environments (Fitzpatrick and Keegan 2007; McCauley et al. 2015; Braje et al. 2017). Evidence of dramatic impacts on local terrestrial flora and fauna have been noted across spatial scales, from small islands to entire continents. Even relatively small groups of subsistence hunters and gatherers have been shown to alter local ecosystems across numerous Pacific islands, most notably New Zealand and Easter Island (Rapa Nui) (Duncan et al. 2002; Nagaoka 2002; Hunt and Lip 2006; Allentoft et al. 2014). Additionally, human arrival across Europe, Asia, and the Americas has also been suggested as the principal trigger in many terrestrial megafauna extinctions (Nogués-Bravo et al. 2008; Lorenzen et al. 2011; Sandom et al. 2014; Faurby and Svenning 2015).

Unlike terrestrial ecosystems, human exploitation resulting in marine population collapses and altered ecosystem dynamics are almost entirely concentrated from the 16th century onward, during the most intensive and industrialized phase of modern commercial exploitation (Hofman and Bonner 1985; Aulsebrook 1998; McCauley et al. 2015). Examples include the extinction of the Great Auk (Garðarsson 1984; Petersen 1995; Fuller 1999), Stellar's sea cow (Anderson 2001), Canadian Maritimes walrus (McLeod et al. 2014), and the collapse of New Zealand fur seals (Dussex et al. 2016; Salis et al. 2016), and numerous species of cetaceans (Hilborn et al. 2003; Baker and Clapham 2004). Earlier impacts on marine species have, until recently, been assumed rare due to the abundance, resilience, size of oceans, and a technological barrier to exploitation that have delayed the use of marine resources by subsistence hunters (Malakoff 1997; Anderson 2001; McCauley et al. 2015). There has been, however, growing recognition of potential preindustrial human impacts on marine ecosystems, yet these have still received little attention and generally relate to subsistence-based hunting (Erlanson and Rick 2010). Therefore, the extinction of the Icelandic walrus provides an exceptionally early example of hunting not driven solely for subsistence, but rather international demand for valuable trade commodities including walrus ivory, oil, and skin sold across medieval markets in Europe, the Middle East, and Asia.

Conclusion

Our results support the existence of a unique genetic lineage of walruses in Iceland hunted by the Norse until its local extinction sometime during the 11–12th centuries. As such, it is one of the earliest examples of a population collapse following commercialized European hunting, occurring centuries before the majority of documented large-scale marine population collapses resulting from industrialized exploitation. Our results suggest that commercial hunting and economic incentives as early as the Viking Age were of sufficient scale and intensity to result in significant, irreversible ecological impacts on the marine environment.

Materials and Methods

Written Historic Records, Place Names, and Skeletal Remains

The historic records of walrus in Iceland were obtained from old literature relating to the Settlement period (870–930 AD) and Commonwealth period (930–1262). The primary literature sources were the Sagas of Icelanders (*Íslendingasögur*) and the Book of Settlements (*Landnámabók*), both available online by the Netutgafan Ltd (<https://www.snerpa.is/net/isl/isl.htm>).

Special attention was given to the Icelandic names *rostungur* and *rosmhvalur* (old Norse/early Icelandic for walrus), as well as *hvallátur*. On one hand, we refer here to *Speculum regale*, the Kings mirror (*Konungs skuggsjá*) written in 13th century AD, informing that walrus (Icelandic pl: *rostungar*) were listed among whales (Icelandic pl: *hvalir*), as well as among large fishes (Larsson 1917; Lárusson 1955). On the other hand, we maintain that the word *hvallátur* most probably means “whale” haul-out, as the original meaning of the word *látur*, is “a place where someone lies or rests at” (Kristjánsson 1984; Murray-Bergquist 2017). We also used previous work and compilations of walrus place names by Þorvaldur Thoroddsen (Thoroddsen 1911), Bjarni Einarsson (Kristjánsson 1984), Lúðvík Kristjánsson (Kristjánsson 1986), and Ólafur Halldórsson (Halldórsson 2010), along with maps, other printed material, and online digital sources.

Information on skeletal remains of walrus were mainly based on data registers compiled from various sources, including the work of Þorvaldur Thoroddsen (Thoroddsen 1911) and Lúðvík Kristjánsson (Kristjánsson 1986), written annals, newspapers, articles, and personal communication.

Historic and Ancient Walrus Samples

A total of 38 walrus skulls and tusks were sampled from the collections at the Icelandic Institute of Natural History, Icelandic Museum of Natural History, Natural History Museum of Denmark, and private collections (supplementary material 1, Supplementary Material online). Of these, 26 Icelandic tusks were drilled at the Icelandic Institute of Natural History, and the remaining 12 samples were drilled by the Icelandic Museum of Natural History at farms near the finding site in Snæfellsnes. An additional 47 samples from across the North Atlantic (including one from Iceland) were collected from the Canadian Museum of History, Natural History Museum of Denmark, and Nunavut Department of Culture and Heritage, Canadian Museum of Nature (supplementary material 1, Supplementary Material online). The additional samples from across the North Atlantic were included to provide comparisons to other historic and ancient populations of walrus (supplementary material 1, Supplementary Material online). All samples for radiocarbon and genetic analyses were taken from separate individuals, verified by distinct radiocarbon dates, mitochondrial genome haplotypes, sampling location, bone element type, size, and attachment to skull (with respect to tusk samples).

All samples collected from the Natural History Museum of Denmark were drilled using a Dremel Micro 8050 at 5,000 rpm under strict clean-lab conditions, to obtain between 100 and 200 mg of powder at the GeoGenetics laboratory, University of Copenhagen, Denmark. Samples collected on site in Iceland were drilled using a Black & Decker and Proxxon MICROMOT 230/E at 5,000–6,500 rpm, with ~500 mg taken to obtain sufficient material for both genetic and radiocarbon analyses.

Radiocarbon Dating

Out of 38 bone powder samples, 34 were successfully radiocarbon dated at Aarhus AMS Centre, Department of Physics and Astronomy from Aarhus University, Denmark. These samples represent all accessible specimens from the Icelandic Museum of Natural History and the Icelandic Institute of Natural History for which permissions to sample sufficient material could be obtained. Dates were calibrated with OxCal (v4.1) (Bronk Ramsey 2010) using the marine model calibration curve (Marine 13; Reimer et al. 2013) with a local delta-R of 111 ± 14 C years taken for Northern Iceland (Ascough et al. 2007; Batt et al. 2015). Non-Icelandic reference samples were dated in broad cultural categories based on archaeological cultural designation, stratigraphic placements, and contemporaneous terrestrial faunal radiocarbon dates.

Extraction of Ancient and Historic DNA

For all material included in this study, DNA was extracted from 90 to 338 mg using the protocol outlined in the supplementary information of Dabney et al. (2013). Where possible 200 mg of fine powder was used, however, in some cases, small chunks had to be cut, resulting in weights of >250 mg. For these small pieces, a short bleach-wash was included prior to extraction as per Boessenkool et al. (2017). Extractions and all subsequent laboratory work steps were completed under strict clean lab conditions following published guidelines regarding a dedicated aDNA laboratory physically removed from any amplification, the use of negative controls (included throughout the drilling, extraction, library build, and amplification process), reproducibility, confirmation of expected fragment length profiles, and damage patterns (Cooper and Poinar 2000; Gilbert et al. 2005). Additionally, all laboratory equipment, materials, and surfaces were continually sterilized using UV radiation, bleach, and ethanol. Any negative control with DNA present according to automated electrophoresis quantification (see below) was included in pools submitted for sequencing. Not a single read from any negative control was found to align to the walrus genome.

Sequencing of the Mitochondrial Control Region

A 450-bp region of the noncoding CR of the mtDNA was successfully amplified for 26 Icelandic samples with polymerase chain reaction (PCR) using the primers DL-2f (CTGACGCCCTACCATTTCATA) and DL-3R (TTATGTGTGATCATGGGCTGA) specified in Lindqvist et al. (2009). Each amplification reaction of 15 µl included 1.5 µl of DNA extract, 1× OneTaq Master Mix (New England Biolabs),

0.2 μ M of each primer (10 μ M IDT, Leuven, Belgium). Thermal cycling conditions were an initial denaturing phase of 5 min. at 94 °C, followed by the annealing phase comprising 40 cycles (30 s at 94 °C, 1 min at 57 °C and 1 min at 68 °C) and a final extension phase at 68 °C during 5 min. For the 22 samples that did not amplify in the first round, amplifications were repeated using primer sets containing additional newly designed internal primers; rost_CR-R1 (GAGGCCTGG TGATCAAGCTT) with DL-2f and rost_CR-F1 (CTTGATC ACCAGGCCTCGAG) with DL-3R. PCR products were SANGER sequenced in both directions by Genewiz (Takeley, United Kingdom).

Extract concentration and fragment lengths were analyzed using automated electrophoresis on a TapeStation 2200 (Agilent Technologies, Santa Clara). The highest yielding Icelandic extracts with fragment length profiles corresponding with expectations of aDNA and showing limited contamination (i.e., no long fragment length peaks indicating bacterial contamination) were then prepared for shotgun sequencing to obtain entire mitochondrial genomes (see below).

Sequencing of Mitochondrial Genomes

Mitochondrial genomes were generated for the ten highest yielding Icelandic extracts, as well as an additional 46 samples from across the North Atlantic. Libraries were built following Carøe et al.'s (2018) protocol, with the adapter concentration modified to match extract concentrations. Samples were amplified in three independent 25 μ l reactions using 3 μ l of library. Final concentrations were of 1 \times of 10 \times Pfu Turbo Reaction Buffer (Agilent Technologies), 1.25 U of PfuTurbo Cx Hotstart DNA Polymerase (Agilent Technologies), 0.02 mg BSA, 8.75 pmol each of a unique combination of forward and reverse indices (IDT) and 3.125 pmol of each dNTP. Thermal cycling conditions were an initial denaturing phase of 2 min at 95 °C, followed by the annealing phase (cycles of 30 s at 94 °C, 1 min at 57 °C, and 1 min at 68 °C) and a final extension phase for 10 min at 70 °C. Cycle number was determined from extract concentration and duplicate qPCR (Stratagene Mx 3000) runs following the same set-up as described earlier but with 1 μ l of SyBR green fluorescent dye. Shot-gun sequencing was performed using single-end Illumina HiSeq4000 and HiSeq2500 at the National High-throughput DNA Sequencing Centre, University of Copenhagen.

Control Region Bioinformatic Analyses

Comparisons of ancient and contemporary walruses from across the North Atlantic were conducted to explore whether Icelandic walruses went extinct or fled resulting in admixture with surrounding populations. Existing mitochondrial haplotypes for the CR were downloaded from NCBI GenBank from previously published research (supplementary material 7, Supplementary Material online).

All previously published CR sequences were divided in seven populations according to geographic location: North Canada (CN n = 88), Thule, North-West Greenland (n = 8), Canadian Maritimes (CM n = 28), East Greenland (GE

n = 104), Svalbard (Sv n = 55), Franz Josef Land (FJ n = 24), and Pechora Sea (PE n = 47). Additionally, 16 Pacific Ocean and five Laptev Sea sequences were included as outgroup comparisons. Sequences were manually aligned in MEGAX (v10.0.5) (Kumar et al. 2018).

Haplotypes were determined in R using “pegas” (Paradis 2010), with the sample containing the fewest number of unknown sites chosen as the representative sample for each haplotype. Unique haplotypes were deposited in GenBank (accession: MK 671142–671149). A haplotype network using TCS network (Clement et al. 2002) was created in PopArt (v1.7) (Leigh and Bryant 2015) for all sequences that had no more than one ambiguous or missing base. Pairwise genetic distances (K2P) between all sequences were calculated in R using “ape” (Paradis 2010). Sequence divergence between samples was summarized with pairwise Φ_{ST} , using the AMOVA function in “pegas” (Paradis 2010) with statistical significance of the estimate obtained after 1,000 permutations. A multidimensional scale plot was constructed in R to visualize the ordinations of the samples based on the Φ_{ST} values.

Mitochondrial Genome Bioinformatic Analyses

Shotgun sequenced data were demultiplexed and run through the Paleomix (v1.2.13) (Schubert et al. 2014) BAM pipeline. This involved indexing raw reads and reference sequences using SAMtools (v1.3.1) (Li et al. 2009) and bwa (v0.7.15) (Li and Durbin 2009), before removing adapter sequences, ambiguous, and low-quality bases with Adapter Removal (v2.2.0) (Schubert et al. 2016). Reads shorter than 25 bp were excluded and minQuality was set to 30. Remaining reads were then aligned with bwa to a reference Atlantic walrus mitochondrial genome (NCBI accession: NC_004029.2). Due to initial poor mapping of the entire D-loop (including the CR), this alignment was repeated with only the D-loop and then the remaining mitochondria. Output .bam files were indexed with SAMtools and PCR duplicates removed by MarkDuplicates (Broad Institute). MapDamage (v2.0.6) (Jónsson et al. 2013). Mapdamage scores could not be determined using mitochondrial alignments for many samples, however, characteristic postmortem damage (supplementary material 8, Supplementary Material online) of ancient DNA was confirmed by running the above steps with the entire nuclear genome. Summary statistics were examined, particularly measures of clonality, endogenous content, and raw read number.

In addition, we obtained raw reads from previously published walrus mitochondrial genomes from Star et al. (2018). These paired-end data were subjected to the same bioinformatic pipeline as outlined above, except that overlapping reads were merged and mate pairs identified using SAMtools.

Once aligned, haploid mitochondrial genotypes were called for each sample using SAMtools and BAQ computation (Li 2011) against the reference Atlantic mitochondria, implemented through angsd (v0.921) (Korneliussen et al. 2014). Bases were called according to frequency for each individual and restricted to sites with at least a depth of three reads per sample. Reads that had multiple best hits or with a

flag >255 were removed. Output files were then converted as phylip files for further phylogenetic analyses using “phylotools” (Zhang et al. 2010) implemented in R (v3.5.1) (R Core Team 2018). Only mitochondrial genomes with at least 60% of called bases were included for subsequent analyses, calculated using “stringr” (Wickham 2015) and “phylotools” in R. This reduced the total number of newly generated mitochondrial genomes for phylogenetic analysis from 56 to 37. Haplotype and nucleotide diversity was calculated using DnaSP v.6. (Rozas et al. 2017) (supplementary material 9, Supplementary Material online). The mitochondrial genomes used in phylogenetic analysis were deposited in GenBank (accession: MK 671108-41).

SNPs from the entire mitochondrial genome that were unique to at least one Icelandic sample were recorded following manual curation using MEGA. The positions of these SNPs were then compared with available modern data to determine if any “Icelandic” haplotypes are now found in modern populations of other geographic areas.

Phylogenetic Analysis

For CR and the entire mitochondrial genome data sets, bModeltest (Bouckaert and Drummond 2017) implemented in BEAST2 (v.2.5.1) (Bouckaert et al. 2014) was used to determine the appropriate evolutionary model, gamma rate heterogeneity, and invariable sites. Guidance on BEAST2 analyses and set-up were obtained from Barido-Sottani et al. (2018). Samples were run with a relaxed exponential clock (Drummond et al. 2006) with a $7.0E^{-8}$ prior (entire mitochondrial genome) and $7.5E^{-8}$ (CR) as per Star et al. (2018) under both a Coalescent Exponential Population model and Extended Bayesian Coalescent Model with chain lengths of 50,000,000. Tip ages were included for the entire mitochondrial genomes, as the midpoint age of each cultural period or 95.4% confidence interval of radiocarbon dating (supplementary material 1, Supplementary Material online). Analyses were repeated for the entire mitochondrial genome after partitioning (1st, 2nd, and 3rd codons as well as noncoding regions). Partitioning was checked manually in MEGA (Kumar et al. 2018). A combined data set using the 3rd and noncoding partitions was used for subsequent analyses to show intraspecific population structure.

For each phylogeny, three separate runs were performed to randomize starting seed, and output combined using LogCombiner (v1.8.0). Log files were checked in Tracer (v1.7.1), with ESS values of at least 200 and agreement between runs required for convergence. Consensus trees were selected using TreeAnnotator (v2.5.1) after a 10% burn-in and viewed with FigTree (v1.4.3). All programs are implemented in BEAST2 (v.2.5.1) (Bouckaert et al. 2014).

Phylogenies were also attempted for CR data, however, no population-level structure was resolved and all branches had extremely low support values, concordant with findings by Star et al. (2018). An Extended Bayesian Skyline Plot was also completed using BEAST2 for CR data, using the same approach as described earlier to attempt to infer population trajectories across the sampled time span.

Map and Figures

Maps were made using QGIS (v3.4.2) (2018) using a coastline shapefile from the National Land Survey of Iceland (2018). Figures prepared in Inkscape (v0.92) (Inkscape Team 2018).

Supplementary Material

Supplementary data are available at *Molecular Biology and Evolution* online.

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Author Contributions

X.K., S.P., H.J.M., M.T.O.: conceived, designed, and funded the study. X.K., S.P., H.J.M.: sample procurement; X.K., M.F.C.: genetic laboratory work; X.K., S.P., M.T.O.: coordination; S.P., H.J.M.: coordination of radiocarbon analyses; M.F.C.: specimen descriptions; X.K., S.P.: bioinformatic analyses; A.P., Icelandic Museum of Natural History: compilation of data registers; A.P., B.F.E., H.J.M., S.P.: collection of walrus skeletal records; A.P., B.F.E., H.J.M.: place names; M.F.C.: preliminary data exploration; X.K.: creation of figures; X.K.: compilation of extended data and supplementary material; X.K.: writing of first version of article; S.P., B.F.E., A.P., P.J., M.F.C., M.T.O., H.J.M.: writing small portions of text and commenting on numerous draft manuscripts. All authors read and approved of the final version of the article.

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